

Interspecific variations in fish occupancy and abundance are driven by niche characteristics in a monsoon-climate river basin

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Acknowledgements

This study was funded by grants from the National Key Research & Development Program of Yunnan Province (202203AC100001), the Biodiversity Survey and Assessment Project of the Ministry of Ecology and Environment, China (2019HJ2096001006), and the China Three Gorges Corporation (0799574). The authors declared that there was no conflict of interest, and no permit was required for this research.

Abstract

Aim: The interspecific relationships between species occupancy and abundance have been broadly studied in terrestrial systems, however, the causes underlying this relationship in freshwater fishes remain poorly addressed. The main aims of this study were: (a) to examine the occupancy-abundance relationship in 62 fish species in a monsoon-climate river; (b) to determine the relative importance of species niche, functional traits, and phylogenetic relatedness in shaping the occupancy-abundance relationship.

Location: The Chishui River, the Yunnan-Guizhou Plateau and the Szechwan Basin, China.

Taxon: Freshwater fishes.

Methods: A linear model was used to test the relationship between distribution and mean abundance across fish species. The outlying mean index analysis was performed to estimate niche breadth and niche position parameters for each fish species. In addition, using principal coordinates analysis, we created four trait vectors describing the similarity of species' traits. Fish phylogeny was obtained from a global molecular phylogenetic tree of actinopterygian fishes. We used a combination of linear models, commonality analyses, and boosted regression trees to evaluate the relative effects of the niche metrics, traits, and phylogenetic relatedness on occupancy and abundance.

Results: Fish occupancy was strongly ($R^2 = 0.749$) and positively correlated with mean abundance in the Chishui River. Niche parameters, especially niche position, were the main determinants of variation in occupancy (e.g. total contribution of niche position and breadth using commonality analyses: 0.587 and 0.318) and abundance (0.323 and 0.151) across species. Furthermore, traits and phylogeny had little to no effect on fish occupancy (0.034 and 0.037) and abundance (0.021 and 0.003).

Main conclusions: Freshwater fishes in the Chishui River fit the common macroecological pattern of positive relationship between occupancy and abundance. Niche parameters, but not traits and phylogeny, are the primary correlates of riverine fish distribution and abundance.

Key words: Freshwater fishes, Functional traits, Regional occupancy, Mean abundance, Niche properties, Phylogeny

1. Introduction

Understanding why some species are abundant while others are scarce, and why some species are widely distributed while others are narrowly distributed, are central goals of macroecology and biogeography (Brown, 1984; Gaston et al., 2000). It has long been recognized that species regional occupancy and mean abundance are not independent of each other (Lawton, 1993) but are typically positively correlated (Gaston & Lawton, 1990). This positive relationship has been well documented for various taxonomic groups (e.g. moths, invertebrates, plants, and birds), in different ecosystems, and at different spatial scales (e.g. from single drainage basin to different biogeographic regions) (Gaston et al., 2000; Heino & Tolonen, 2018; Quinn, Gaston, Blackburn, & Eversham, 1997; Vela Díaz et al., 2020). Indeed, this pattern has even been suggested to be one of the most pervasive patterns in macroecology (Gaston et al., 2000). Occupancy-abundance relationships (OARs) have received much interest among ecologists because they provide important links between local and regional scales, and between ecological processes across multiple species (Webb, Barry, & McClain, 2017). Moreover, understanding OARs may be important in practice due to the information they offer for the conservation and management of species (Gaston et al., 2000; Lawton, 1993).

During the past decades, the emphasis in the research of OARs has shifted from pattern

documentation to exploring the potential underlying mechanisms (Gaston, Blackburn, & Lawton, 1997; Heino & Tolonen, 2018). To date, nine general hypotheses have been put forward to explain positive OARs, including sampling artefact, phylogenetic non-independence, range position, aggregated spatial distribution, niche breadth, habitat availability, density-dependent habitat selection, metapopulation dynamics, and vital rates (Gaston et al., 2000; Gaston et al., 1997). Among these hypotheses, the first four represent potential artefacts, whereas the others refer to putative ecological processes underlying occupancy and abundance. Regarding the role of these mechanisms in determining OARs, there are ongoing debates, however. Instead of focusing on any single mechanism, some authors have also suggested that determining the relative roles of different mechanisms is a more fruitful avenue of research (Tales, Keith, & Oberdorff, 2004; Verberk, Van Der Velde, & Esselink, 2010).

Species niche breadth and niche position are often found to be key mechanisms driving occupancy and abundance (Heino & Grönroos, 2014; Heino & Soininen, 2006; Tales et al., 2004). Both niche properties reflect the degree to which environmental conditions meet species habitat requirements and resource use, yet their role in explaining OARs may be different (Gaston et al., 2000). This is because the niche breadth hypothesis postulates that species able to exploit a wide variety of resources and/or tolerate a broad range of abiotic environmental conditions should be more locally common and regionally widespread than species restricted to using particular sets of resources and/or prefer specific environmental conditions (Brown, 1984). In other words, the broader the species niche, the wider the regional distribution and the higher the average local abundance. Instead, the niche position (i.e., how typical the environmental conditions in which a species occurs are of the full set of available conditions) hypothesis assumes that species able to utilize the most common environment in a region are typically locally abundant and widely distributed (Venier & Fahrig, 1996). Contrastingly, species preferring sites that are regionally uncommon in terms of environmental conditions should have low local abundance and narrow regional distribution. Overall, a given species showing high occupancy and abundance may thus have either a large niche breadth or non-marginal niche position. Previous studies have found support for either the niche breadth hypothesis, including studies on pond macroinvertebrates (Verberk et al., 2010), diatoms (Teittinen, Weckström, & Soininen, 2018), and lake fish, (Faulks, Svanbäck, Ragnarsson-Stabo, Eklöv, & Östman, 2015), or the niche position hypotheses, including studies on breeding birds, (Gregory & Gaston, 2000), riverine fish, (Tales et al., 2004), stream diatoms (Heino & Soininen, 2006), and macroinvertebrates (Rocha et al., 2018).

Functional traits can also affect occupancy and abundance (Heino & Grönroos, 2014; Vilmi, Karjalainen, Wang, & Heino, 2019), because species sharing a similar suite of functional traits should also show similar OAR patterns (Poff, 1997). The idea underlying this assumption is that species traits should be tightly associated with habitat and resource use because the environment selects for certain trait combinations but not necessarily species *per se* (Heino & Tolonen, 2017; Wang, Jiang, Zhou, Dai, & Song, 2019), thereby influencing OARs. However, findings from recent empirical studies are somewhat mixed (Heino & Grönroos, 2014; Vilmi, Karjalainen, et al., 2019). For instance, Miranda and Killgore (2019) found that some fish guilds indeed show different slopes of the OAR. However, Heino and Tolonen (2018) found that biological traits similarity only has minor effects on occupancy and abundance of littoral macroinvertebrates. Finally, because of their phylogenetic relatedness, any two species might not be considered as independent data points in the OAR analysis, owing to inflation of the degrees of freedom available for testing statistical

significance (Gaston et al., 2000). This inflation, if strong enough, is likely to yield a false conclusion that a significant OAR exists (Gaston et al., 2000). More importantly, it is widely acknowledged that species' responses to the environment result from trait combinations rather than individual traits (Verberk, Van Noordwijk, & Hildrew, 2013), which is probably associated with phylogenetic relatedness of species. Thus, closely-related species are likely to share similar functional traits, thereby exhibiting similar levels of occupancy and abundance (Blackburn, Gaston, & Gregory, 1997).

In the freshwater realm, fishes are typically common in most systems and contribute to several ecological processes, such as controlling the abundance of other organisms through predation and competition (Matthews, 1998; Villéger, Brosse, Mouchet, Mouillot, & Vanni, 2017). However, fish biodiversity is threatened by various human-induced pressures on freshwater ecosystems (Albert et al., 2021). Hence, the distribution and abundance of fish should deserve specific attention because understanding these species features is important in guiding fish conservation and population management. Given that only a few studies have reported freshwater fish OARs, we know relatively little about the prevalence of this pattern and potential underlying mechanisms in these organisms. The paucity of studies studying OAR in freshwater fish may result from the rarity of such relationships in nature, lack of suitable datasets, as well as lack of interest in these topics (Miranda & Killgore, 2019). To our knowledge, only 11 studies have reported OARs for fish (Table S1.1). Among these studies, eight have found evidence for positive OARs (Gotelli and Taylor, 1999; Tales et al., 2004; Granado-Lorencio, Araujo Lima, and Lobón-Cerviá, 2005; Taylor et al., 2006; Passy, 2012; Faulks et al., 2015; Miranda and Killgore, 2019; Granzotti, Cassemiro, Agostinho, and Bini, 2021), while the others have reported non-significant or even negative OARs (Gaston and Lawton, 1990; Pyron, 1999; Roney, Kuperinen, and Hutchings, 2015). Furthermore, few studies have explored the relative roles of multiple mechanisms in driving fish occupancy and abundance (Tales et al., 2004; Passy, 2012). More importantly, all past works were concentrated on American and European freshwater ecosystems, whereas there is a lack of studies from Asian rivers (Table S1.1). Studying new regions and surveying fish assemblages located within different species pools that are affected by different evolutionary histories, might help to explore whether the proposed hypotheses that apply to terrestrial taxa (Gaston et al., 2000) and other aquatic organisms (Heino & Tolonen, 2018) could also be generalized to fish faunas.

Here, we characterized fish OAR and aimed to untangle the relative importance of niche breadth, niche position, functional traits, and phylogenetic relatedness in accounting for such an association in the Chishui River, China. We posed the following questions: First, is there a positive OAR in the fish fauna of the Chishui River? Second, which variables (i.e., niche parameters, traits, and phylogeny) best account for variation in regional occupancy? Third, which variables best account for variation in abundance? Fourth, which variables best account for variation around the OAR? Building on findings of previous studies, we expected that niche features are the main correlates of fish occupancy and abundance in our system. However, we could also expect that traits and phylogenetic relatedness play an additional role in explaining variation in occupancy and abundance, although their effects might be weaker compared with the niche features.

2. Material and methods

2.1 Study area

The study system comprises the whole area of the Chishui River (27°20'–28°50'N, 104°45'–106°51'E, Figure 1), China. The focal river basin is approximately 437 km long and covers a

drainage basin area of 20,440 km². This area is characterized by a subtropical monsoon climate and precipitation is generally concentrated between June and September (Jiang, Xiong, & Xie, 2017). The main land types in this area are farmland, forest, shrub, and grassland (Wang et al., 2018). Because of its abundant environmental resources, the region provides important habitats and refuges for a wide array of endemic species on both terrestrial and freshwater environments (e.g. *Ampelocalamus scandens*, *Sinocrossocheilus labiatus*, and *Leptobotia elongata*) (Wang, Jiang, Huang, Zhang, & Yu, 2007; Zhong, Gou, Liu, Zhu, & Dai, 2021). In addition, without evident flow regulation and no dam was constructed in the mainstem of river channel, the system offers an excellent opportunity to examine the fit of ecological theories with empirical patterns found in freshwater biota (Jiang et al., 2017). Overall, the studied river is a hotspot of biodiversity, requiring guidelines for its assessment and conservation.

2.2 Biological sampling

In April of 2007, field surveys of fish assemblages were conducted at 31 locations. The dry season was chosen since this allowed for greater efficiency in the collection of fish, as well as to avoid seasonal variation. Each sampling location was a 200-500 m stretch encompassing all types of geomorphological forms in the river channel (e.g. riffles, runs, and pools). Two commonly utilized electrofishing protocols were applied to maximize the capture of fish. Specifically, for shallow water locations, fish specimens were collected by means of backpack electrofishing. The crew sampled the reach in an upstream direction with two passes. For non-wadable areas, boat electrofishing was applied by moving the boat slowly in a downstream direction. The combination of these two methods is necessary to optimize sampling efforts in large rivers due to their high heterogeneity of habitats (Liu, Wang, Zhang, Liu, & Wang, 2020; Schmera et al., 2018). Nevertheless, the two sampling techniques have different catch efficiencies and could thus yield different estimates of fish abundance and occupancy. However, a recent study has illustrated that this practice may increase variance in OARs but does not strongly change the significance or strength of correlations (Miranda & Killgore, 2019). All collected fish were identified to species level, measured, and weighed. Most individuals were released to the sampling sites, and a subset of fish species was fixed in 7% formalin for final preservation.

Several environmental variables were recorded *in situ* after fish collection (Table S1.2). Water temperature (°C), pH, dissolved oxygen (mgL⁻¹), and conductivity (μScm⁻¹) were measured by using a multi-parametric probe (WTW Multi 340i). Water depth (m) and channel width (m) were calculated using a depth sounder, and a Leica CRF900 rangefinder camera, respectively. An altimeter was used to measure altitude (m). Current velocity (ms⁻¹) was determined using a flowmeter device. The percentage of substrate particle size was visually estimated and divided into four types: sand, silt, cobble, and boulder.

2.3 Functional traits

We chose nine functional traits associated with functions played by fish (i.e., food acquisition, mobility, nutrient budget, reproduction, and defense against predation) (Villéger et al., 2017) and can be used to portray species response to the environment: body length, growth rate, lifespan, trophic level, age and length at maturation, body shape, trophic guild and vertical position (Table 1). We selected these traits because they have been widely used in studies investigating the functional diversity of fish faunas in China (Cheng et al., 2014; Jiang, Brosse, Jiang, & Zhang, 2015; Wang et al., 2019). Functional traits were mainly gathered from FishBase (Froese & Pauly, 2014).

We first calculated multi-trait dissimilarity using function gawdis in the ‘gawdis’ package (v.0.1.0;

de Bello, Botta-Dukát, Lepš, & Fibich, 2021). Then, we performed principal coordinates analysis (PCoA) to obtain ‘trait vectors’, i.e., PCoA axes, which represented trait similarity among species. It is advisable to use this approach, since recent studies have shown that abundance and occupancy might not respond independently to a single trait, but trait combinations instead (Verberk et al., 2013) that can be captured using trait vectors (Heino & Tolonen, 2018; Vilmi, Tolonen, Karjalainen, & Heino, 2019). We used the first four trait vectors for further analyses, since Mantel test demonstrated that Euclidean distance based on them was strongly correlated with “gawdis” distance of the original nine traits ($r = 0.931$, $p = 0.001$).

2.4 Phylogenetic data

We obtained fish phylogeny from the phylogenetic tree recently reported by Rabosky et al. (2018), which provided the most comprehensive and time-calibrated phylogenetic information on ray-finned fishes. In the Chishui River, all 13 families and 49 genera were found to be present in the phylogeny, whereas 10 species were absent and were added here at the genus basal node. The resulting phylogeny (Figure S1.1) was fully resolved at the family and genus level and well resolved at the species level, which has been proved to be appropriate for community phylogenetic studies (Li et al., 2019).

To account for phylogenetic relatedness, we computed Moran’s eigenvectors from the phylogeny using the `me.phylo` function in the ‘`adephylo`’ package (v.1.1-11; Jombart & Dray, 2010). If the tree has n tips (species number), $n-1$ vectors will be produced. Phylogenetically similar species have closer values. The first vectors are those with maximum positive autocorrelation, while the last vectors are those with maximum negative autocorrelation. We retained the values from the first eigenvectors as a phylogenetic covariate for further analyses.

2.5 Calculation of niche position and niche breadth values

To quantify niche characteristics for studied fish species, the outlying mean index (OMI) analysis was performed (Dolédec, Chessel, & Gimaret-Carpentier, 2000). The derived OMI index measured the ‘niche position’ of species, which depends on the niche deviation from the distribution of a theoretical species that can tolerate the most average environmental conditions and is uniformly distributed across sites (Dolédec et al., 2000). Specifically, a high OMI value means that a species has a marginal niche position, whereas species having low OMI values have central or non-marginal niches. In addition to the OMI index, this method also provides values of species tolerance (Tales et al., 2004), which estimates the range of species distribution in the space of the sampled environmental gradients. High values of species tolerance indicate wide niche breadth, while low tolerance values denote narrow niche breadth (Heino, 2005).

We log-transformed and standardized environmental variables, and applied Hellinger transformation for abundance data to downweight the effects of rare species in the OMI analysis (Marino et al., 2020). Dissolved oxygen and current velocity were removed from the OMI analysis due to their significant relationships with trophic level. We also removed species that occurred only in one site because the OMI and tolerance values for such species are likely to be misleading (Vilmi, Tolonen, et al., 2019). After this, 62 fish species distributed at least at two sites were retained. OMI analysis was run using the `niche` function available in the ‘`ade4`’ package (v.1.7-13; Dray & Dufour, 2007) (Figure S1.2).

2.6 Statistical analyses

The proportion of sites occupied by species and mean abundance averaged across all sites were employed as a measure of occupancy and abundance, respectively. Occupancy and abundance were

logit, and logarithmically transformed, respectively, to approximate normal distributions. To answer the first question we proposed, we used a linear model to relate occupancy and mean abundance. Then, to answer our second to fourth questions, three separate linear models were constructed to explore the relative effects of the niche metrics, four trait vectors, and one phylogenetic vector on occupancy and abundance, respectively. Residuals of the occupancy-abundance relationship were studied as a fourth response variable, as it depicts occupancy when the effect of abundance has been removed (Heino & Tolonen, 2018; Vilmi, Tolonen, et al., 2019). Niche position and niche breadth were both logarithmically transformed due to their skewed distribution.

To complement the linear model, we also performed commonality analyses (Ray-Mukherjee et al., 2014). Typically, regression coefficients are used in linear models to help rank the predictor variables according to their contribution in the regression equation. Yet, confounding effects of predictors may prevent finding the best predictor among all available predictors. Regression commonality analysis was therefore introduced to tackle this problem by decomposing the variance of R^2 into the unique, common, and total contributions of each predictor to response variables, as has been done before (Heino & Tolonen, 2018). This method may be particularly useful when predictors are correlated, as it can explicitly identify the magnitude and location of multicollinearity and suppression in regression models. Commonality analyses were run using `regr` function in the ‘`yhat`’ package (v.2.0-0; Nimon, Oswald, & Roberts, 2013).

We used the D statistic (Fritz & Purvis, 2010) and the Pagel’s λ (Pagel, 1999) to measure phylogenetic signals in categorical and continuous traits, respectively. If D approaches 0, the trait is distributed as expected under the Brownian motion model of evolution, whereas large values for λ (close to one) suggest a strong phylogenetic signal (Pagel, 1999; Fritz & Purvis, 2010).

To assess phylogenetic uncertainty, we conducted a supplementary analysis using the 100 possibilities for phylogenies reported by Rabosky et al. (2018). Specifically, we calculated phylogenetic vectors based on each of the 100 trees and retained the first vectors as predictors for occupancy and abundance, and repeated the analysis with the residuals of occupancy after the effect of abundance on occupancy is removed. The same analysis was repeated but this time after excluding the species that were not available in the genetic tree of Rabosky et al. (2018).

Finally, we used boosted regression tree (BRT) analysis to more fully understand the relationship between response variables (occupancy and abundance) and their predictors (Elith, Leathwick, & Hastie, 2008). BRTs have no need for prior data transformation or elimination of outliers, can fit complex nonlinear relationships, and can automatically handle interactions between predictors (Elith et al., 2008). In this case, BRTs were fitted to a Gaussian distribution to obtain comparative results with those of linear models. Based on the suggestions by Elith et al. (2008), the following parameters were used for BRT: `tree.complexity=5`, `learning.rate=0.001`, and `bag.fraction=0.5`. A slower learning rate is preferable, conditional on the number of observations and time available for computation. The BRT analyses were performed by ‘`dismo`’ package (v.1.1-4; Hijmans, Phillips, Leathwick, & Elith, 2021). All statistical analyses were conducted in R version 3.6.1 (R Core Team, 2019).

3. Results

A total of 62 fish species were recorded during the field surveys. Species occupancy varied from 6.452% to 96.774%, and mean abundance of fish varied from 0.065 to 12.29. *Zacco platypus*, *Opsariichthys bidens*, *Hemibarbus labeo*, and *Spinibarbus sinensis* were the most abundant and widely distributed species, whereas *Squaliobarbus curriculus*, *Ancherythroculter nigrocauda*,

Hemiculter leucisculus, *Chanodichthys erythropterus*, and *Sarcocheilichthys nigripinnis* were fish with low occupancy and abundance.

We found that the first trait axis was positively correlated with growth rate, but negatively correlated to body length, lifespan, and age/length at maturation. Trophic level was negatively related to trait vector 2 (Table S1.3; Figure S1.3). Categories of trophic guild, body shape, and vertical position also showed a positive or negative association with the first and second axis (Table S1.3; Figure S1.3). Note that only the first two trait vectors were mentioned as they captured most information in the original traits.

Phylogenetic signals were significantly related to growth rate, lifespan, length at maturation, trophic level, and several categories of trophic guild and vertical position, indicating that these traits were conserved phylogenetically (Table S1.4).

Treating species as independent data points, we found that occupancy was positively associated with mean abundance, which accounted for 74.9% variation in occupancy (Figure 2). Thus, species that occurred at a large number of sites also tended to maintain high abundance, while species occurring at a limited number of sites showed low abundance (Figure 2).

The linear model showed that predictors explained 68.8% of interspecific variation in fish occupancy (Table 2). Of the predictor variables examined, niche position was the most important factor affecting occupancy. Occupancy was significantly and negatively associated with niche position, but positively to niche breadth and trait vector 2. The regression commonality analyses also supported this result, as niche position (unique and total contributions: 22.2% and 58.7%) played a larger role than niche breadth (3.5% and 31.8%) and trait vector 2 (3.9% and 0) in explaining occupancy (Table 2).

In comparison to the model of occupancy, the linear model of mean abundance had relatively lower explanatory power, with niche metrics, trait vectors, and a phylogenetic covariate explaining 41.3% of the variation (Table 3). Among all predictor variables, niche position was significantly negatively related to fish abundance. Moreover, we unexpectedly found that niche breadth, trait vectors, and phylogeny not significantly accounted for any variation in abundance. This result was further confirmed by the commonality analysis. As the unique and total contributions of niche position to abundance were 16.4% and 32.3% (Table 3), whereas for the other predictors the two figures were < 3% and < 15.1%, respectively.

The linear regression analyses demonstrated that niche position, niche breadth, trait vectors, and phylogenetic relatedness explained 41.8% of the variation in the residuals of the OAR for fish (Table 4). We found that residuals of the OAR were only negatively and significantly associated with niche position, with the unique and total contributions being 5.8% and 30%, respectively (Table 4).

Similar patterns were found as those of our best phylogeny, no matter the 100 trees from Rabosky et al. (2018) (Table S2.1 and Figure S2.1, 2.2, 2.3 in the supplementary materials), or a purely genetic tree (Table S3.1, 3.2, 3.3 and Figure S3.1 in the supplementary materials) was used to calculate phylogenetic vectors.

The BRT analyses explained 68.8% and 31.3% of deviance in occupancy and abundance, respectively (Figure 3). The BRT analyses demonstrated rather similar results to those of linear models, as niche position was the most important predictor of occupancy (relative contribution: 57.4%) and abundance (60%) (Figure 3). Nevertheless, according to partial dependency plots, niche breadth also exceeded the relative importance of over 20%, showing a nonlinear relationship with occupancy and abundance (Figure 3). Four trait vectors and the phylogenetic covariate made only

minor contributions to fish distribution and abundance, with their relative importance varying from 2.5 to 5.4% and 2.9 to 5.2%, respectively (Figure 3).

4. Discussion

We found a significant positive OAR of fish in the Chishui River, suggesting that this pervasive pattern also occurs in riverine fish. This is the first time, to our knowledge, that a positive OAR has been documented for fish species in Asian rivers. The relationship we observed here was rather strong, with the coefficient of determination (R^2) being 0.749. In a seminal review published 25 years ago, Gaston (1996) collated findings from over 90 papers, covering a diverse array of taxa from a wide range of habitats and geographic regions, and summarized that significant R^2 values ranged from 0.075 to 0.756. Thus, the R^2 value we reported here is at the upper end of this range, indicating that freshwater fish fit this general macroecological pattern. Our results are also generally consistent with previous investigations of fish OARs in European and American freshwater systems (Miranda & Killgore, 2019; Tales et al., 2004; Taylor et al., 2006).

Potential artefacts need to be considered before evaluating biological factors underlying the OAR. Firstly, it is well known that locally scarce species, initially thought to be regionally narrowly distributed, may show considerably wider distributions after increasing sampling efforts (Gaston et al., 1997; Heino, 2008). However, this is highly unlikely in our study because the electrofishing method we used has a good catchability efficiency for the ichthyofauna in our study region (Wu, Wang, He, & Cao, 2011). Therefore, most species that actually occurred at a site should have been captured by the sampling method we used. Secondly, phylogenetic non-independence can also be a major problem, but this is not the case in our study, as we found no evidence for the role of the phylogenetic covariate in accounting for interspecific variation in fish occupancy and abundance. Thirdly, range position of species might be another mechanism underlying the positive OAR. Species whose center of geographic range occurs in the study area can be assumed to show high abundance and occupancy, while those whose center of geographic range is far from overlapping the study area tend to show low abundance and occupancy (Brown, 1984). This hypothesis does not apply in our study, as most of the studied fish species have their center of geographic range across the upper Yangtze River. Furthermore, a recent study indicated that fish are not necessarily most abundant in the center of their geographic range (Dallas, Decker, & Hastings, 2017). Fourthly, the occupancy and abundance of species may be affected by the spatial distribution of individuals (Wright, 1991), but this is unlikely in our study since all fish species in the focal river are heterogeneously distributed across the sampling sites. Moreover, the extent to which this hypothesis pertains to a strict mechanism underlying OARs, rather than being a restatement of the OAR in another form, is questionable (Gaston et al., 2000).

Out of the biological hypotheses, density-dependent habitat selection (O'Connor, 1987) and vital rate (Holt, Lawton, Gaston, & Blackburn, 1997) cannot be directly tested with the current data at our disposal because they require direct information on birth and death rates in local populations, which are not available for the fish species and sites in our dataset. Metapopulation dynamics predict that locally abundant species can easily colonize empty habitats via excessive dispersal (Hanski, 1994), thereby generating a positive OAR. However, our community-level analyses suggested that dispersal limitation rather than excessive dispersal is influential in explaining fish community composition in our system (Figure S1.4). Therefore, metapopulation dynamics may be of minor importance in determining abundance and occupancy. However, given that community-level analysis considers all species at the same time, it is only a coarse proxy of single-species

metapopulation dynamics. This is because each species may show different spatial dynamics and environmental preferences and, therefore, respond independently to abiotic factors (Heino & de Mendoza, 2016).

The habitat availability and niche breadth hypotheses have received widespread support in previous studies, and our results also corroborated these findings. As expected, a significantly negative association between niche position and abundance or distribution was observed, justifying the importance of the niche position hypothesis (Venier & Fahrig, 1996). Thus, riverine fish utilizing common habitats or resources would be widespread and abundant, whereas species restricted to using uncommon habitats or resources would tend to be regionally rare and locally scarce (Tales et al., 2004). Situated in the transitional zone of the Yunnan-Guizhou Plateau and the Szechwan Basin, the Chishui River is characterized by complex river morphology and an extensive elevational gradient, leading to major changes in abiotic and biotic factors along the elevational gradient (Wu et al., 2011). Hence, non-marginal species are typically those that have no preference for certain habitat conditions (e.g. *Z. platypus*, *O. bidens*, *H. labeo*, and *S. sinensis*), which are more abundant and widespread than marginal species that prefer downstream sites (e.g. *S. curriculum*, *A. nigrocauda*, *H. leucisculus*, *C. erythropterus*, and *S. nigripinnis*). This suggests that downstream sites may represent 'atypical' environments for fish in our system. Such findings partly differ from those reported by Tales et al. (2004), who found that fish with high niche positions appeared in downstream areas and those with low niche positions preferred upstream areas. Differences in the spatial variation of environmental conditions may have contributed to the differences between Tales et al.'s (2004) and our study, with headwater streams in their study likely embracing most environmental conditions in the French hydrographic network, whereas local environments vary dramatically along the elevational gradient in the Chishui River. Overall, our results corroborate those of prior works, suggesting that niche position is probably a common mechanism influencing occupancy or abundance of aquatic organisms (Heino & Tolonen, 2018; Marino et al., 2020; Vilmi, Tolonen, et al., 2019). However, it should be noted that most studies (including this study) examining fish OARs are from lotic (river and stream) systems. One study conducted across Swedish lakes suggested that local abundance was mainly positively correlated with habitat and diet breadths of fish (Faulks et al., 2015). As lentic systems (lake and pond) are more patchily distributed in the landscape compared with lotic systems, more research is needed to explore ecological processes creating OARs for lake fish.

Our study also supported the niche breadth hypothesis (Brown, 1984), as fish species with broad niches were more widespread regionally and more abundant locally than species with narrow niches. However, there is no consensus on the generality of this pattern. On the one hand, in a meta-analysis, Slatyer, Hirst, and Sexton (2013) revealed that the positive relationship between niche breadth and range size was maintained across organism groups, measurements, and spatial scales. On the other hand, two recent studies on aquatic invertebrates (Marino et al., 2020) and vascular plants (Vela Díaz et al., 2020) found no positive relationship between niche breadth and occupancy or abundance, which was possibly due to random sampling efforts. An interesting result in our study was that multiple regression analysis found no significant linear relationship between niche breadth and abundance (Table 3), whereas the BRT analyses revealed a nonlinear relationship between them (Figure 3). Thus, complementary methods should be adopted in future studies of fish OARs, as the relationship may be non-linear rather than linear. In addition, the relative importance of niche breadth was secondary to niche position in the BRT analysis in our study. This finding corroborates

the conclusion made by Gaston and Blackburn (2000), but it disagrees with previous studies on stream insects (Siqueira, Bini, Cianciaruso, Roque, & Trivinho-Strixino, 2009), lake fish (Faulks et al., 2015), stream algae (Passy, 2012), and pond diatoms (Teittinen et al., 2018).

The differences between the present findings and other studies might result from methodological problems relating to the estimation of niche breadth. Indeed, niche is a multidimensional concept (Hutchinson, 1957), which can be quantified by multiple ways, but no approach is likely to be optimal (Lawton, 1993). However, we argue that niche breadth in our study mirrors how fish species respond to the range of environmental conditions. Moreover, the number and length of underlying environmental gradients should also be considered (Passy, 2012). In particular, notwithstanding the pronounced elevational gradient, environmental conditions in the present study area were relatively subtle because we focused on a near-pristine river basin. On the contrary, the stream diatom study of Passy (2012) was based on a continental area in the USA, with wide variability in climate, topography, nutrient supply, and human impacts, whereas the pond diatom study of Teittinen et al. (2018) comprised a wide range of limnological characteristics in a subarctic area in Finland.

The functional traits had only marginal effects on fish occupancy and abundance. Specifically, only trait vector 2 was significantly associated with fish distribution. Since trophic level is the strongest correlate of trait vector 2 among the continuous variables, this finding suggests that species at high trophic levels tend to show a narrower range than species at low trophic level groups, possibly because of energy constraints and their position in the food web (Miranda & Killgore, 2019). As for categorical traits, body shape, trophic guild, and vertical position are closely related to fish mobility and food acquisition strategies (Villéger et al., 2017), indicating that species with high dispersal rates and efficient food acquisition ability probably have wider distributions than fish with low swimming speed and weak food acquisition ability. There are three potential reasons why the similarity of functional traits was not strongly related to fish occupancy or abundance. First, in comparison to species niche properties, functional traits might be of little importance in predicting variation in occupancy and abundance of aquatic organisms at regional scales (Rocha et al., 2018; Vilmi, Tolonen, et al., 2019). This explanation is somewhat uncertain, thereby deserving further comparative research at different scales and in different kinds of ecological systems. Second, it is possible that we used the wrong functional traits and/or measured an inadequate set of environmental variables (Heino & Tolonen, 2018). However, we highlight that the chosen traits covered major niche dimensions and functions played by freshwater fish (Villéger et al., 2017), and they are closely related to abiotic conditions (Cheng et al., 2014). Also, the measured environmental variables are known to shape fish communities in this river (Wu et al., 2011). Thus, we are confident that methodological limitations cannot explain why trait vectors were not strongly correlated with occupancy or abundance. Third, relatively weak support for the importance of traits in shaping occupancy and abundance may stem from spatial processes, which may weaken species-environment relationships and explain why trait vectors were not strong correlates of occupancy and abundance.

In general, closely related species, sharing a set of phylogenetically conserved traits, can be expected to show a similar level of abundance and occupancy (Blackburn et al., 1997). Yet, we found no evidence for the influence of phylogenetic relatedness on fish distribution and abundance. Four reasons may account for the lack of support for phylogenetic relatedness. First, excluding it as a potential artefact, phylogenetic relatedness did not violate assumptions of independence across species and, therefore, did not drive the directionality and strength of OAR in our study. However,

485 this idea deserves further evaluation in freshwater ecosystems, as most of the previous investigations
486 on this topic were based on taxonomic information as a proxy for real phylogeny (Heino & Tolonen,
487 2018; Vilmi, Karjalainen, et al., 2019). Second, some traits (e.g. body length and trophic guild)
488 might not show strong phylogenetic signals but they might be more evolutionarily labile (Poff et al.,
489 2006), being variable in phylogenetically distant lineages. Therefore, phylogenetic similarity may
490 not play a vital role in affecting distribution and abundance (Quinn et al., 1997), as was suggested
491 by our findings. Third, functional traits and phylogeny may represent different ecological processes,
492 and traits are only partly characterized by phylogeny (Cadotte, Carboni, Si, & Tatsumi, 2019).
493 Therefore, it was not surprising that phylogenetic relatedness was not a strong predictor of
494 occupancy and abundance in this study. Fourth, the spatial scale may be associated with the
495 importance of phylogeny in accounting for variation in occupancy and abundance. As we only
496 focused on a single drainage basin, the spatial scale might be too small for the influence of
497 phylogenetic relatedness on occupancy and abundance to be visible. Indeed, it has been proposed
498 that species environmental niches are more important at local and regional scales (Heino &
499 Grönroos, 2014), while historical factors overcome their effects at continental scales (Brändle &
500 Brandl, 2001). Hence, if we extended the fish investigations to a very large spatial extent with
501 distinct historical and evolutionary processes among regions (e.g. different rivers in China), a strong
502 phylogenetic signal in species distribution and abundance could be found (Heino & Tolonen, 2018).

503 The main applied implications of our results are threefold. Firstly, incidence data may be used as
504 a proxy for abundance data in biodiversity research (Foggo, Frost, & Attrill, 2003). However, recent
505 studies have questioned the accuracy of incidence-based data as they underestimated the role of
506 dominant and abundant species (Dai, Jiang, Wang, Matsuzaki, & Zhou, 2020). Yet, dominant and
507 abundant species are typically those with wide distributions, and thus we argue that incidence data
508 may provide adequate information and serve as a proxy for abundance data. Secondly, OAR is an
509 important tool for identifying threatened species (i.e., species with low abundance and restricted
510 distribution) and determining the minimum number of priority areas aiming at protecting all species
511 (Gaston et al., 2000). In addition, our results suggest that conservation programs intended to
512 preserve rare species should prioritize the conservation of marginal habitats. Finally, the positive
513 OAR has the potential to predict the spread of invasive species (Gaston et al., 2000), because once
514 invasive species are successfully established in some areas, their local abundance increases
515 correspondingly.

Table 1 Functional traits selected to study occupancy and abundance patterns of fish in the Chishui River basin, China (modified from Wang et al., 2019).

Trait	Type	Unit / categories
Age at maturation	Continuous	Years
Body shape	Categorical	Anguilliform, Compressed, Cylindrical, Dorso-ventrally flattened, Oval
Growth rate	Continuous	Year ⁻¹
Length at maturation	Continuous	Centimeter
Lifespan	Continuous	Years
Body length	Continuous	Centimeter
Trophic guild	Categorical	Detritivore, Herbivore, Invertivore, Omnivore, Piscivore, Planktivore
Trophic level	Continuous	Number
Vertical position	Categorical	Benthopelagic, Demersal

Table 2 Descriptive statistics of multiple regression models for predicting variation in logit-transformed occupancy of fish species. Full model statistics: $R^2 = 0.688$, $F = 16.98$, $P < 0.001$. Additionally, using commonality analysis, unique, common, and total contributions of each predictor variable to the regional occupancy are also shown. Phylo.vector = Phylogenetic vector.

	Estimate	SE	t	p	Unique	Common	Total
(Intercept)	0.461	0.521	0.885	0.380			
Niche position	-2.535	0.409	-6.193	<0.001	0.222	0.365	0.587
Niche breadth	1.747	0.714	2.447	0.018	0.035	0.283	0.318
Trait vector 1	0.016	0.819	0.019	0.985	0.000	0.013	0.013
Trait vector 2	2.566	0.987	2.601	0.012	0.039	-0.039	0.000
Trait vector 3	-0.470	1.051	-0.447	0.657	0.001	0.016	0.017
Trait vector 4	-2.364	1.279	-1.848	0.070	0.020	-0.016	0.004
Phylo.vector	0.158	0.163	0.968	0.337	0.005	0.031	0.037

Table 3 Descriptive statistics of multiple regression models for predicting variation in log-transformed mean abundance across sampling species. Full model statistics: $R^2 = 0.413$, $F = 5.430$, $P < 0.001$. Additionally, based on commonality analysis, unique, common, and total contributions of each predictor variable to the total mean abundance are also shown. Phylo.vector = Phylogenetic vector.

	Estimate	SE	t	p	Unique	Common	Total
(Intercept)	0.788	0.170	4.631	< 0.001			
Niche position	-0.520	0.134	-3.888	< 0.001	0.164	0.158	0.323
Niche breadth	0.226	0.233	0.967	0.338	0.010	0.141	0.151
Trait vector 1	0.233	0.268	0.871	0.388	0.008	-0.007	0.001
Trait vector 2	0.535	0.322	1.661	0.102	0.030	-0.028	0.002
Trait vector 3	0.010	0.343	0.028	0.978	0.000	0.004	0.004
Trait vector 4	-0.640	0.418	-1.531	0.132	0.026	-0.011	0.014
Phylo.vector	0.002	0.053	0.043	0.966	0.000	0.003	0.003

Table 4 Descriptive statistics of multiple regression models for predicting variation in the residuals of the occupancy-abundance relationship of fish species. Residuals of the occupancy-abundance relationship depicts occupancy when the effect of abundance has been removed. Full model statistics: $R^2 = 0.418$, $F = 5.540$, $P < 0.001$. Additionally, based on commonality analysis, unique, common, and total contributions of each predictor variable to the residuals of the occupancy-abundance relationship are also shown. Phylo.vector = Phylogenetic vector.

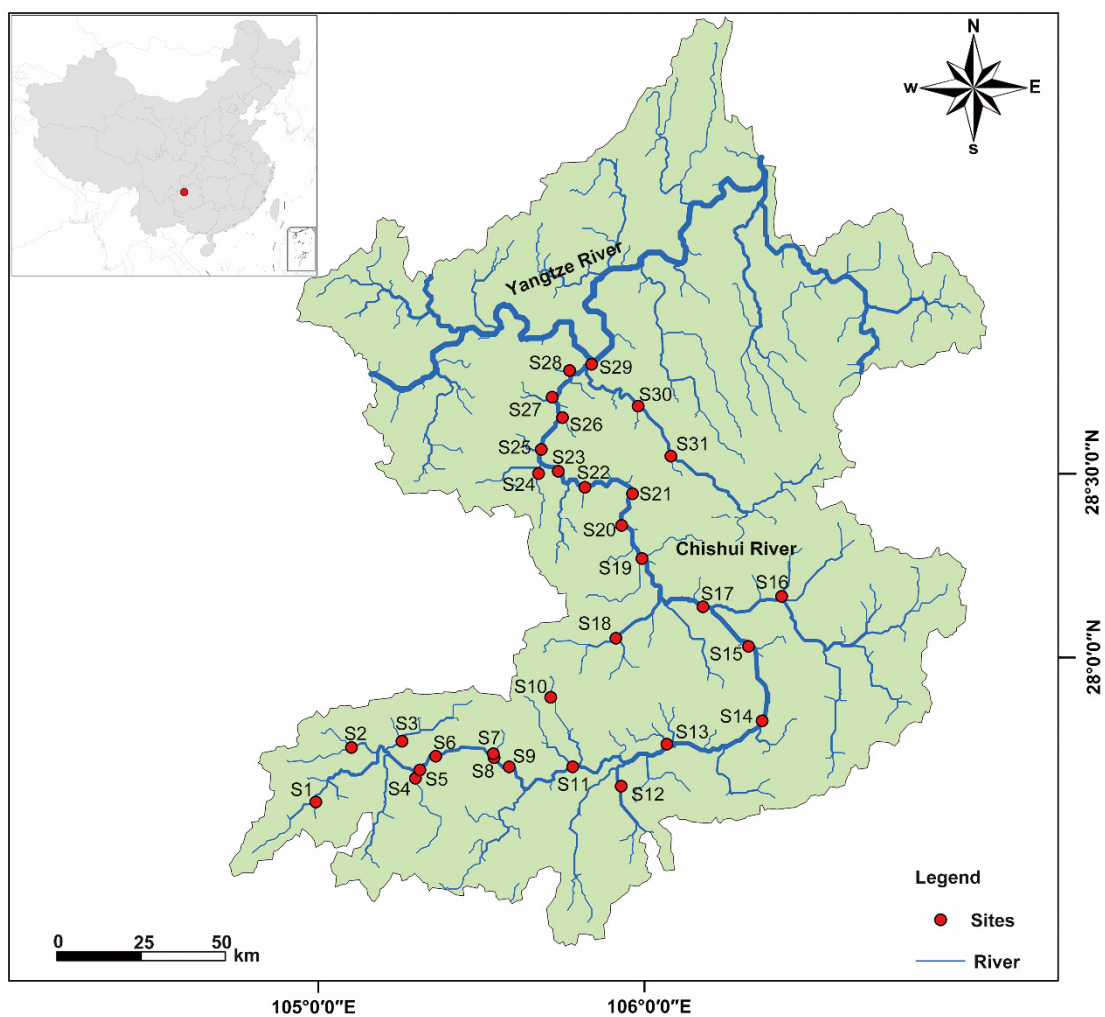
	Estimate	SE	t	p	Unique	Common	Total
(Intercept)	0.089	0.356	0.249	0.805			
Niche position	-0.648	0.280	-2.312	0.025	0.058	0.242	0.300
Niche breadth	0.928	0.488	1.900	0.063	0.039	0.167	0.206
Trait vector 1	-0.831	0.560	-1.482	0.144	0.024	0.057	0.081
Trait vector 2	0.622	0.675	0.922	0.360	0.009	0.002	0.011
Trait vector 3	-0.505	0.719	-0.702	0.486	0.005	0.017	0.022
Trait vector 4	-0.041	0.875	-0.047	0.963	0.000	0.006	0.006
Phylo.vector	0.150	0.112	1.341	0.186	0.019	0.065	0.084

Figure captions:

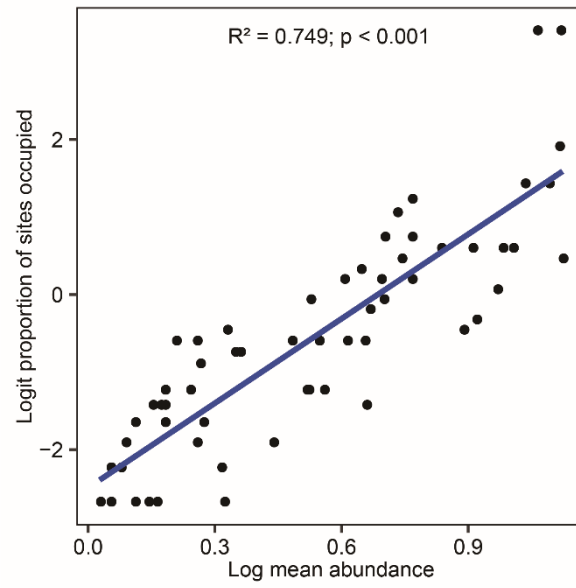
Figure 1 Map showing the 31 sampling sites distributed across the whole Chishui River basin, China. The projection in the map is Asian Lambert conformal conic.

Figure 2 The relationship between occupancy (logit-transformed) and mean abundance (log-transformed) across fish species found in the Chishui River, China.

Figure 3 Results of boosted regression trees showing the partial dependency plots between response variables (a: occupancy; b: abundance) and single predictors describing fish niche parameters, functional traits, and phylogeny in the Chishui River, China. The plots are ranked according to the relative importance of each variable, which is shown in parentheses. Rug plots in each plot indicate the decile distribution of the variable. Phylo.vector = Phylogenetic vector.



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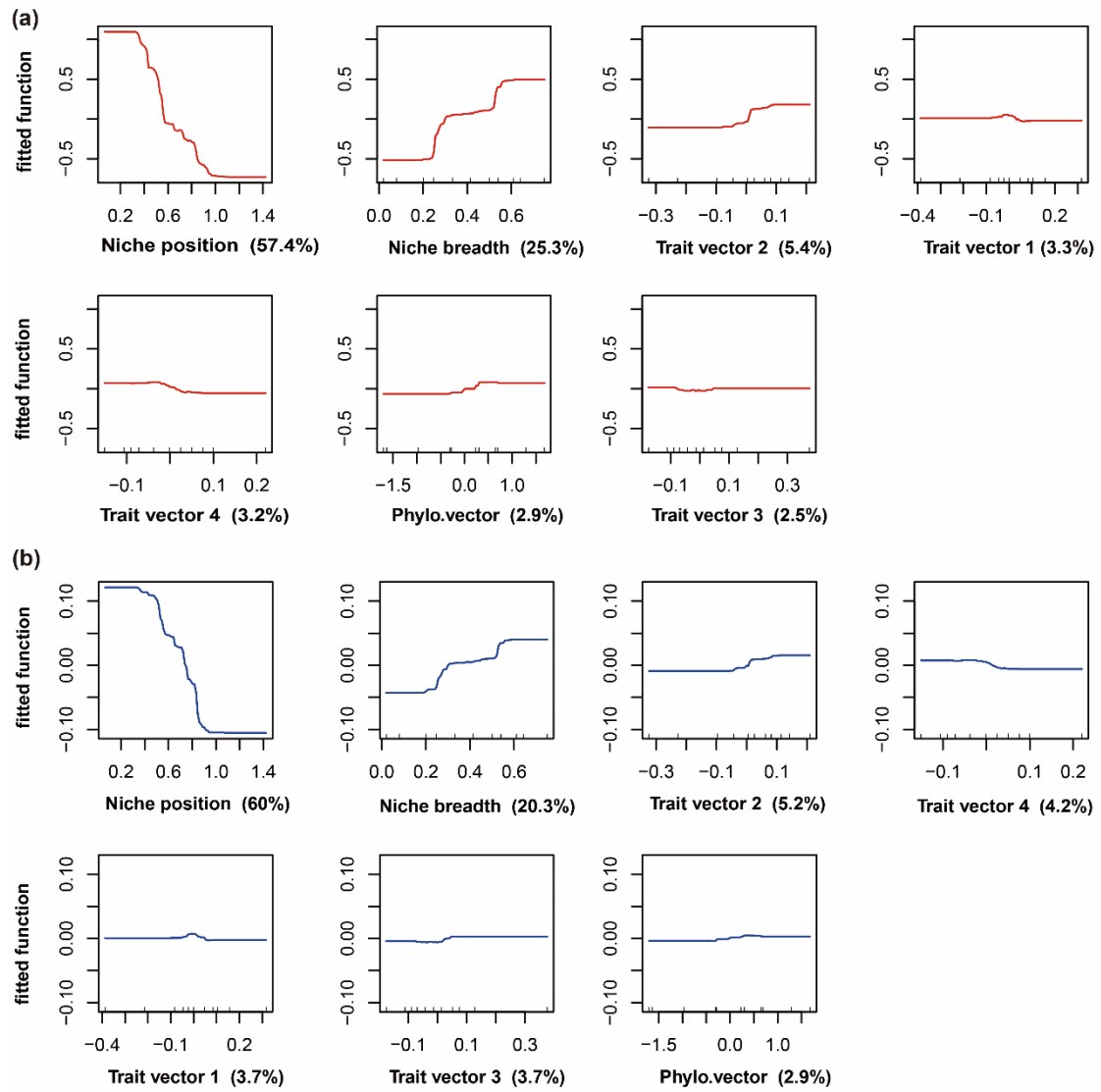
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Data Availability Statement

Relevant datasets used in this study are available from the Dryad Digital Repository (<https://doi.org/10.5061/dryad.3r2280gj9>).

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BIOSKETCH

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Author Contributions: Z.X. and J.W. conceived the ideas. F.L. and J.W. conducted fieldwork and collected the data. Z.X., F.Y., C.X., M.H., and X.Z. analyzed the data. Z.X. led the manuscript writing. J.H. and J.W. made comments on the manuscript. All authors contributed critically to the draft and gave final approval for publication.